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Two new idoteid isopods from Baja California and the Gulf of California (Mexico) and an analysis of the evolutionary history the genus *Colidotea* (Crustacea: Isopoda: Idoteidae)

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Abstract. Two new species of idoteine isopod crustaceans are described from Baja California, *Colidotea wallersteini* new species and *Synidotea francesae* new species (Crustacea: Valvifera: Idoteidae: Idoteinae). The genus *Colidotea* is rediagnosed, a key to the known species presented, and its evolution and historical biogeography described. Both trans-oceanic dispersal and vicariance phenomona appear to have played roles in the establishment of modern distributional patterns of *Colidotea*.

Introduction

The idoteid isopod fauna of the northeast Pacific has, in the past 10 years, come to be quite well known (see Brusca and Wallerstein 1979b for an introduction to the literature). The present study adds 2 new species to this fauna, based on material collected by Dr. D. G. Lindquist (University of North Carolina) and some previously unsorted samples of microcrustaceans at the Allan Hancock Foundation (University of Southern California).

The terminology used in this paper is standard for the idoteid isopod literature (see Menzies 1950 for a summary). The following abbreviations are used: AHF, Allan Hancock Foundation; USNM, National Museum of Natural History; SDNHM, San Diego Natural History Museum.

Systematics

Order Isopoda
Suborder Valvifera
Family Idoteidae
Subfamily Idoteinae

Genus *Synidotea* Harger, 1878

The systematics and biogeography of the genus *Synidotea* were reviewed by Menzies and Miller (1972), who recognized 36 valid species and subspecies, 8 of which occur in California. Iverson (1972) described a ninth species from California (*S. media*). Brusca and Wallerstein (1979a) presented new distributional records for *S. harfordi* Benedict, 1897, which at that time was believed to be the southernmost ranging species of the genus in the northeastern Pacific. They noted its disjunct occurrence: central California to Magdalena Bay (SW Baja California), Mexico, reappearing again in the central Gulf of California, Mexico (2 known records). Brusca and Wallerstein (1979b) reviewed the distributions of the 7 known northeastern Pacific shallow-water *Synidotea*, noting that all but *S. harfordi* were entirely restricted to the cold-temperate waters of the Arctic, Aleutian and Oregonian Provinces. Brusca (in press) discusses phylogenetic

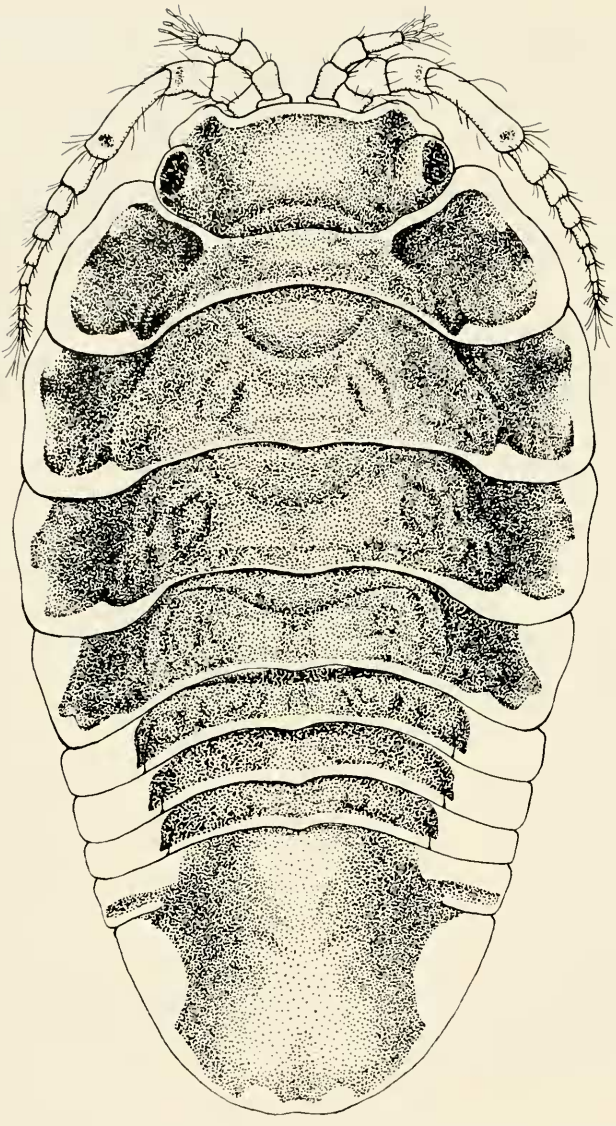

FIGURE 1. *Synidotea francesae* new species. Holotype, AHF 736. Female.

relationships, evolutionary history and zoogeography of *Synidotea,* as well as the 21 other genera of Idoteinae.

Synidotea francesae new species
Figures 1, 2, 3

Types.—Holotype: female, AHF 736; Allotype: male, AHF 736a. Paratypes: 1 female, SDNHM; 1 female, USNM.

Locality.—All specimens from single collection: Mexico, Gulf of California, Sonora, El Golfo de Santa Clara (about 4 miles SE of town); found on sandy beach, "scavenging" on cast up tubes of *Chaetopterus* species (Polychaeta); air temperature 24°C; water temperature (surf) 19°C; 17 April 1973; collected by D. G. Lindquist.

Diagnosis.—Cephalon without horns or other projections; frontal margin convex; eyes bulge outward; body without tubercles or rugae; pleotelson wider than long; per-

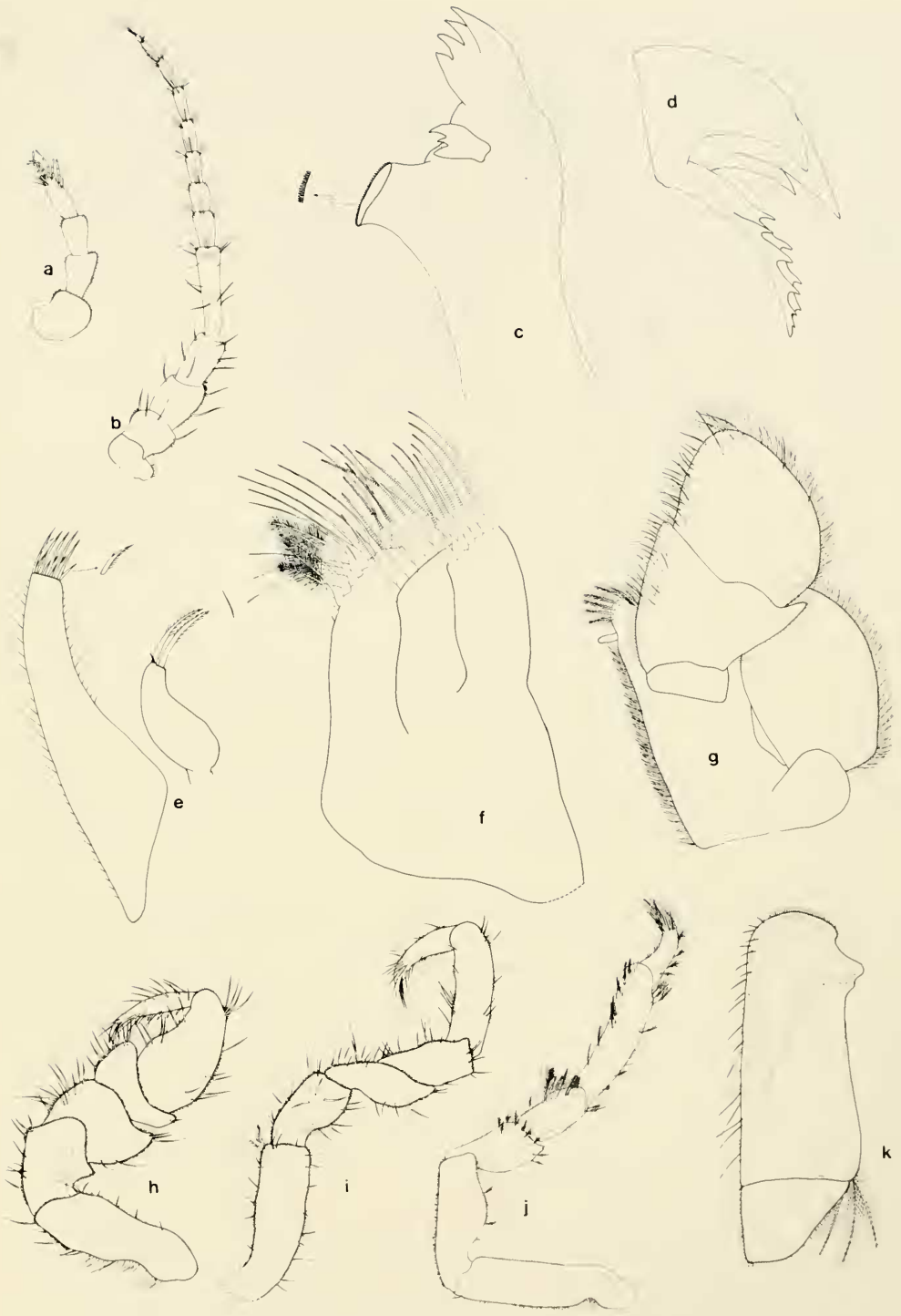

FIGURE 2. *Synidotea francesae* new species. Holotype, AHF 736. Female. a, antenna 1. b, antenna 2. c, left mandible. d, lacinia of right mandible. e, maxilla 1. f, maxilla 2. g, maxilliped. h, pereopod I. i, pereiopod IV. j, pereopod VII. k, uropod.

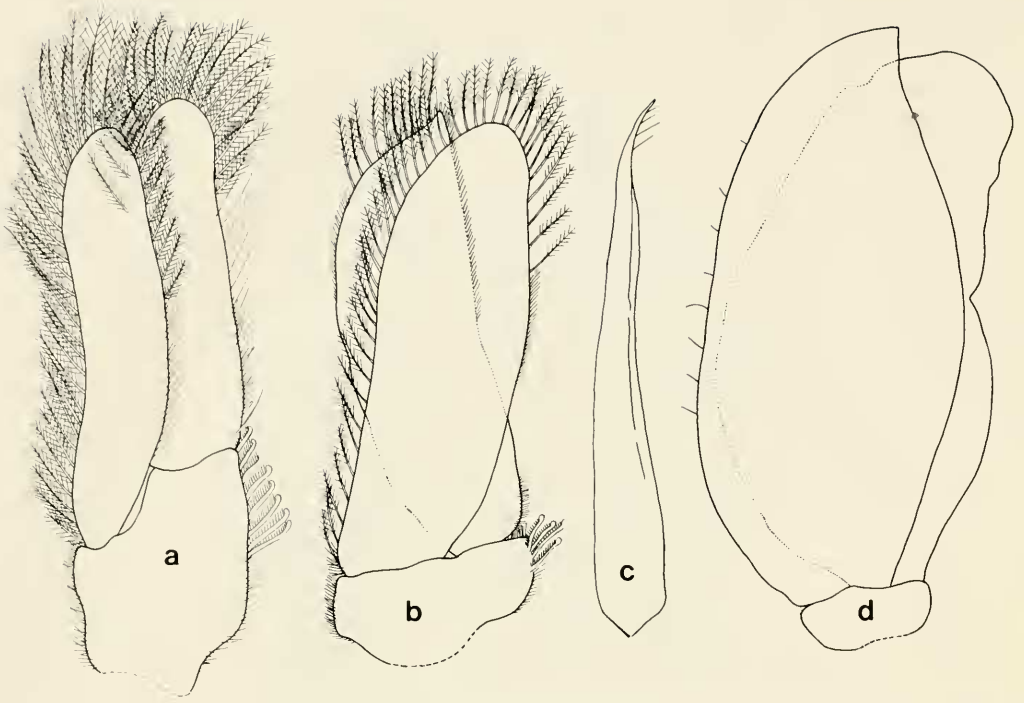

FIGURE 3. *Synidotea francesae* new species. a, pleopod 1 (holotype). b, pleopod 2 (holotype). c, appendix masculinum of pleopod 2, male (allotype). d, pleopod 5 (holotype).

eonites V–VII manifestly shorter than I–IV; median dorsal pattern rounded, as in *S. laticauda*; dorsum with heavy pigmentation.

Description.—Length to at least 6 mm; body ovate and darkly pigmented; dorsum smooth.

Cephalon: Lacking horns or other projections; frontal margin convex, although anterolateral angles somewhat expanded; eyes elevated, on distinct bulges. Antenna 1 with tri-articulate peduncle and uniarticulate flagellum; distal third of terminal article with simple setae and esthetascs. Antenna 2 with 5-articulate peduncle and 8-articulate flagellum; all articles with setae; articles 4 and 5 of peduncle each with distinct distal patch of chromatophores; flagellum quite short, extended only to pereonite II. Maxilliped typical for the genus, with single coupling hook. Maxilla 1 typical for the genus; inner lobe with 2 stout plumose setae; outer lobe with 6 long simple setae and 4 short pectinate setae. Maxilla 2 typical for the genus, with plumose, simple and comb setae as figured. Mandible with 4-toothed incisor and large molar process, the latter smooth on outer margin and toothed on inner margin; lacinia mobilis of left mandible 3-toothed; lacinia of right mandible 3-toothed but with additional large serrate spinelike process.

Pereon: Manifestly elevated along middorsal line; entire dorsal surface with dark pigmentation, except along lateral margins. Pereonites I–IV large, long and without dorsal coxal plates; pereonites V–VII small, short, and with large dorsal coxal plates, visible in dorsal aspect by presence of faint suture lines just median of edge of chromatophore pattern; all pereopods form ventral coxal plates that meet in midline of sterna. Median dorsal pattern of pereonites II–IV (*sensu* Menzies and Miller 1972) with rounded posterior margins. Pereonites IV–VII slightly produced along posteromedial margin. Pereopod I with dactyl nearly as long as propodus.

Pleon: Posterior border with faint indentation, otherwise evenly convex. Pleon (=pleotelson) width equal to length, or up to 1.5 times wider than long. Pleopods 1–3

TABLE 1. Principal attributes distinguishing *Colidotea* and its sister-group, *Synisoma*, from each other and from all other genera of Idoteinae.*

	Colidotea	*Synisoma*
Flagella of second antennae	multiarticulate	multiarticulate
Number of articles in maxillipedal palp	4	4
Appendix masculina (of male)	long, arising from base of endopod (of second pleopod)	long, arising from base of endopod (of second pleopod)
Lacinia mobilis	very large; as large or nearly as large as incisor process	very large; as large or nearly as large as incisor process
Pleon	relatively short; much less than ⅓ total body length	relatively long; ⅓ or more total body length
Pleomere fusion	all pleomeres fused; one pair lateral incisions present	all pleomeres fused; no lateral incisions remain
Eyes	very small (except in *C. findleyi*); set on lateral margins of cephalon	very small; set on lateral margins of cephalon

* For comparable data on the other 20 genera of Idoteinae see Brusca (in press).

with plumose marginal setae, decreasing posteriorward; pleopods 4–5 without plumose marginal setae. Uropod with 3 stout plumose setae at junction of protopod and lamella. Appendix masculinum of male simple, with weakly grooved inner margin and a few distal setae; penes entirely fused into large tongue-like flap.

Etymology.—*Synidotea francesae* is named in honor of Frances Runyan: biological illustrator, horticulturist, and friend.

Discussion.—*Synidotea francesae* is similar to *S. laticauda* Benedict, 1897, and *S. harfordi* Benedict, 1897 (both known from California shores), in having a smooth dorsum with a characteristic medial dorsal pattern, evenly convex lateral margins on the body somites, elevated (bulging) eyes, and notch at the apex of an otherwise evenly convex pleotelson. It differs most strikingly from these species in having a pleon as wide or wider than long, a barely perceptable notch at the pleotelson apex (rather than a deep notch), pereonites V–VII manifestly reduced in size, and a distinct dorsal chromatophore pattern. It differs further from *S. laticauda* in having an evenly convex frontal margin, a 4-toothed incisor on the mandible, and shorter antennae. It differs further from *S. harfordi* in having rounded posterior margins on the medial dorsal pattern of pereonites II–IV, shorter antennae, and a coupling hook on the maxillipedal endite.

Of the 18 species of *Synidotea* now known from the eastern Pacific, only *S. francesae* is a regular resident of warm waters (i.e., the Eastern Pacific Zoogeographic Region); all others are temperate or polar species. The genus is worldwide in distribution but notably absent from the New World tropics. Brusca and Wallerstein (1979b) and Wallerstein and Brusca (1982) hypothesized that this absence is due to the inability of *Synidotea* species to develop certain morphological (size; body spination) and life history (early reproduction; predator avoidance behaviors) adaptations that have allowed successful radiation in this region by other genera (e.g., *Erichsonella, Eusymmerus, Parasymmerus*), and that any species of Idoteidae that may be found successfully inhabiting the warm coastal waters of the tropical eastern Pacific would have had to evolve some of these adaptations. In the subtropical waters of the Gulf of California, *S. francesae* has evolved at least 1 (small size) if not more (e.g., early reproduction) of these attributes which presumably have played a role in its ability to survive the predation-intense summers of this region. Menzies and Miller (1972) state that the mean length of the 8 Arctic species of *Synidotea* is 18.8 ± 2.6 mm, while the mean length of the 5 tropical species then known (all from the Old World) was 8.0 ± 2.2 mm. Temperate species fall between these two extremes. By comparison, the largest specimen of *Synidotea francesae* examined is only 6 mm in length.

Genus *Colidotea* Richardson, 1905

The genus *Colidotea* was briefly reviewed by Brusca and Wallerstein (1979b). The genus now contains 4 species: *C. rostrata* (Benedict), southern California; *C. findleyi* Brusca and Wallerstein, Baja California; *C. edmondsoni* Miller, Hawaii; and *C. wallersteini* new species, Baja California (Fig. 7). Brusca (in press) discusses the phylogeny, evolutionary history and zoogeography of *Colidotea* and its sister-group, *Synisoma* Leach. Both genera are restricted to warm-temperate and subtropical waters of the New World (*Colidotea*) and Old World (*Synisoma*). Table 1 summarizes the principal features that distinguish these 2 genera from one another and from all other genera of Idoteinae.

A reexamination of the 4 known species of *Colidotea* warrants an expanded diagnosis of the genus and a key to the species, as follows.

Diagnosis.—Idoteinae with body compact, pereon merging smoothly with pleon. Cephalon with anterolateral angles produced; with or without a medial cephalic process or spine; eyes lateral. Second antennae with flagella comprised of a few, or a dozen or so articles, the number increasing somewhat with age (length). Maxillipedal palp of 4 free articles, apical article large and ovate; epipod present; endite with or without coupling hooks. Mandible with large lacinia mobilis, nearly as large, or as large as incisor process. Pereon with coxal plates present on segments II–VII; coxae may or may not be visible in dorsal aspect, or may be visible only on posteriormost pereonites. Pleon comprised of single piece, with one pair of lateral incisions (=suture lines); pleon length less than ⅓ total body length; uropods uniramous. Appendix masculinum of male arising from base of pleopod 2 endopod. Uropods uniramous.

Key to the Species of *Colidotea*

1. Cephalon with medial spine or process, which may or may not project over supra-antennal line 2
– Cephalon without medial spine or process 3
2. Cephalic process bifurcate (2-pronged); frontal process subacute (convex); pleotelson with posterior margin angulate; bases of pereopods with dark chromatophore band ..... *C. edmondsoni*
– Cephalic process simple (single apex); frontal process notched (concave); pleotelson with posterior margin evenly rounded; bases of pereopods without dark chromatophore band ..... *C. rostrata*
3. Frontal process notched (concave); coxal plates hidden in dorsal aspect; pleotelson posterior margin subacute; eyes large; maxilla 2 trilobate ..... *C. findleyi*
– Frontal process not notched, but convex; coxal plates visible on pereonites IV–VII, in dorsal aspect; pleotelson posterior margin evenly rounded; eyes small; maxilla 2 bilobate ..... *C. wallersteini* new species

Colidotea wallersteini new species
Figures 4, 5

Types.—Holotype: male, AHF 452. Paratypes: AHF 4925; SDNHM (1 specimen); USNM (1 specimen).

Locality.—Known from only two localities. Holotype: México, Baja California Norte (Pacific coast), Punta Clara, south Rio Santo Tomás, 18 December 1945, collected by C. Hubbs (H45–217a). Paratypes: México, Guadalupe Island, off N coast of Baja California, Melpomene Cove, intertidal collections, 18 December 1949, collected by R. J. Menzies and D. Reish, *Velero III* (Allan Hancock Foundation), Station No. 1915-49.

Diagnosis.—Body straight-sided; coxal plates visible in dorsal aspect on pereonites IV–VII. Cephalon with supra-antennal line forming 3 points, 1 medial and 2 submedial; frontal process distally convex; antenna 1 flagellum a single article; antenna 2 flagellum with about 9 articles; lacinia mobili present on both right and left mandible; molar

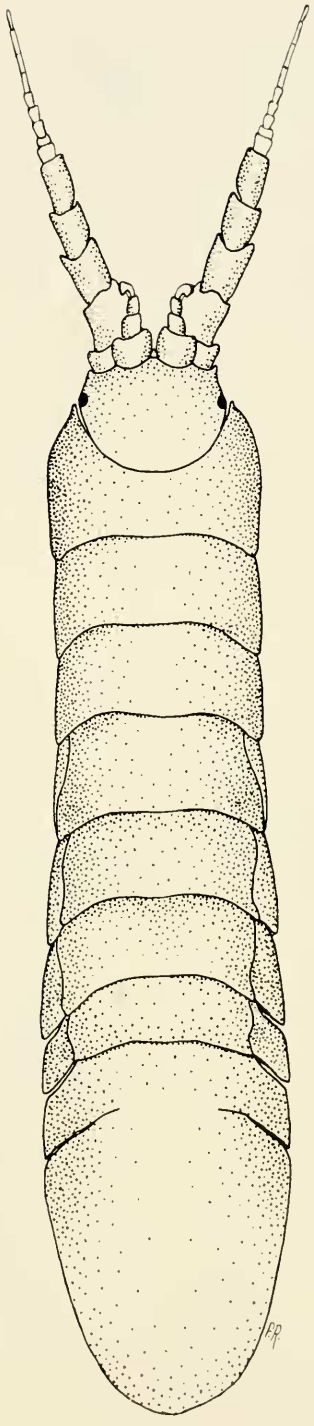

FIGURE 4. *Colidotea wallersteini* new species. Holotype, AHF 452. Male.

process simple, greatly reduced (smaller than lacinia); maxilliped with 2 coupling hooks on right, 1 on left; maxilla 2 bilobate, smaller lobe with 2-jointed apical process terminating in single large seta; posterior margin of pleotelson evenly convex.

Description.—Body smooth, straight-sided, with coxal plates on pereonites II–VII

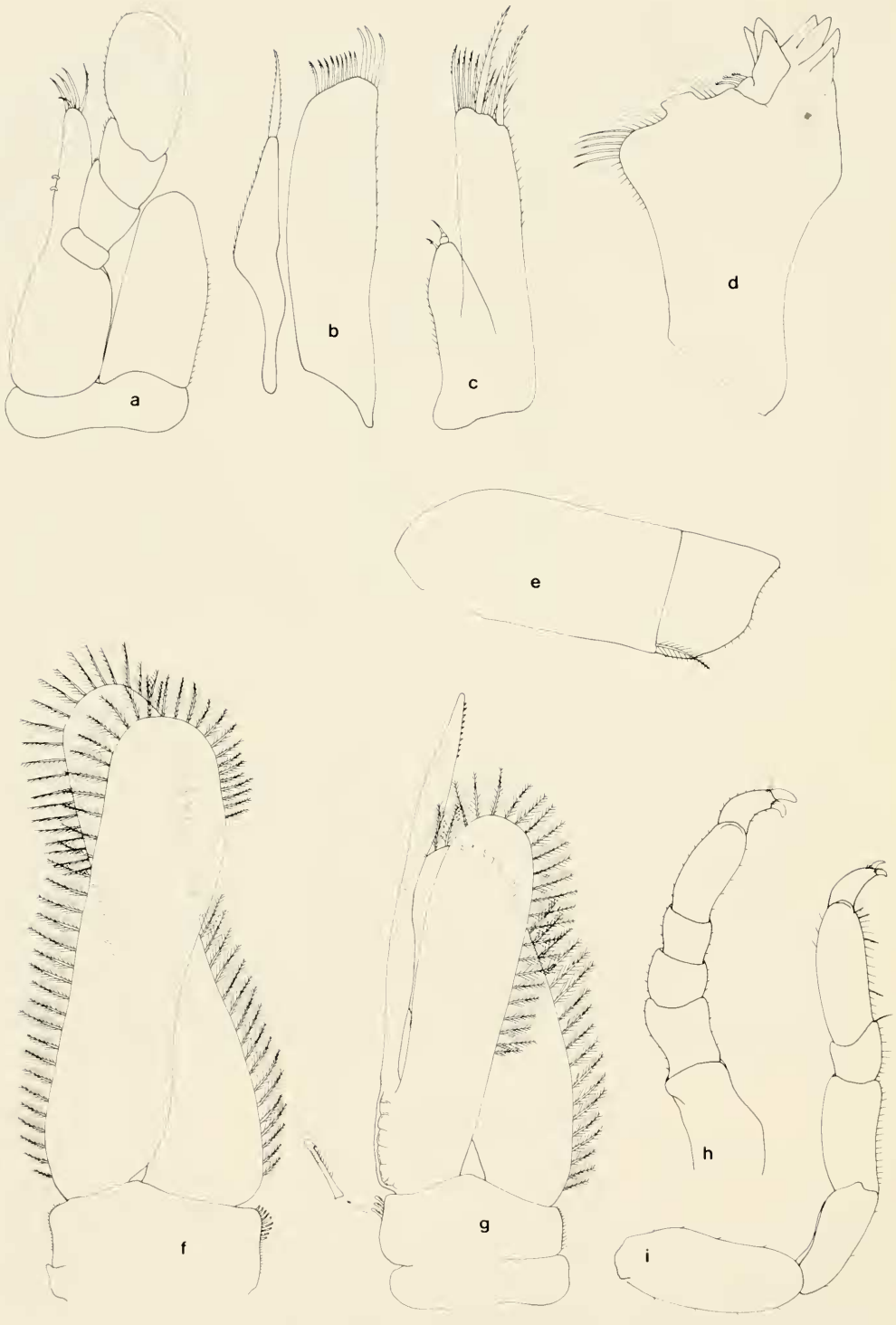

FIGURE 5. *Colidotea wallersteini* new species. Holotype, AHF 452. Male. a, right maxilliped. b, maxilla 1. c, maxilla 2. d, right mandible. e, uropod. f, pleopod 1. g, pleopod 2. h, pereopod IV. i, pereopod I.

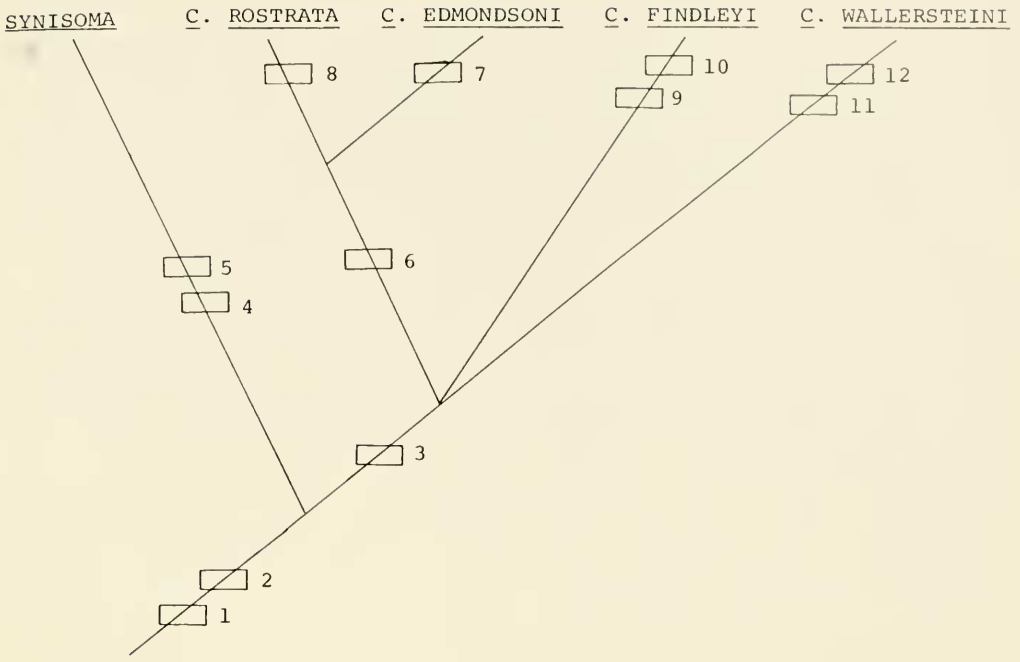

FIGURE 6. Cladistic relationships of the 4 known species of *Colidotea* and their sister-group, *Synisoma*. See Brusca (in press) for character polarity analysis and discussion of relationships outside this clade. Apomorphies indicated are as follow: 1, Reduction from a 5-jointed to a 4-jointed maxillipedal palp. 2, Lacinia mobilis of mandible enlarged, subequal to incisor process. 3, Pleon reduced to a single piece, with a pair of lateral incisions indicating partial fusion of 1 pleomere. 4, Pleon reduced to a single piece, with no remaining lateral incisions. 5, Pleon greatly elongated, ⅓ or more total body length. 6, Cephalon with an anteromedial process. 7, Anteromedial process of cephalon bifid. 8, Adoption of a symbiotic relationship with sea urchins of the genus *Strongylocentrotus*, and associated morphological adaptations (e.g., elliptical body; purple pigmentation). 9, Eyes enlarged. 10, Posterior margin of pleon acute. 11, Second maxillae with only 2 lobes. 12, Typical "spines" of first maxilla outer lobe reduced to 3 slender, stout, simple setae.

(visible in dorsal aspect only on IV–VII). Length to at least 16.5 mm; length 4–5 times width.

Cephalon: Without tubercles or elevations of any kind; broadly immersed in pereonite I; frontal process distally convex. Eyes very small, set on extreme lateral margins. Antenna 1 comprised of 4 articles, fourth being the single flagellar article, with terminal esthetascs. Antenna 2 with 9-articulate flagellum. Mandible with 4-toothed incisor; lacinia with 3 teeth and 3 stout setae; molar process greatly reduced, simple. Maxilla 1 outer lobe with about 9 small apical setae (some of which are comb setae) and 3 stout simple setae; inner lobe ending in single stout setose spine. Maxilla 2 bilobate; larger lobe with 2 very large plumose setae and about 7 smaller setae, some ctenose; smaller lobe with 2-jointed apical process terminating in single large seta. Maxilliped typical for genus; endite with several large apical setae; 2 coupling hooks on right, 1 on left.

Pereon: Smooth, straight-sided, forming continuous line with pleon; pereonite I with anterolateral angles produced to level of eyes, engulfing cephalon. Pereonites gradually increasing in width posteriorly; II–VI subequal in length; I and VII somewhat shorter than others. Well-developed coxal plates present on II–VII, visible in dorsal aspect only on IV–VII. Pereopods I–VII slender and ambulatory, terminating in reflexed, biungulate dactyl; setation simple; ischium of pereopod I grooved to receive basis.

Pleon: Posterior margin of pleotelson evenly convex. Uropods simple; with single large plumose seta at junction of protopod and lamella. Pleopods typical of genus; 1–2 with abundant plumose marginal setae; 3–5 reduced, somewhat fleshy, and either

FIGURE 7. Distributions (locality records) of the known species of *Colidotea*. Open circle = *C. wallersteini*. Closed circle = *C. findleyi*. Triangles = *C. rostrata*. *C. edmondsoni* is endemic to the Hawaiian Islands (not on map).

naked or at most with a few scattered simple setae (as in *C. findleyi*). Appendix masculina large, extended beyond apex of pleopodal lamellae, with short apical spines; base of pleopod 2 endopod "muscularized" just below junction of appendix maxulinum.

Etymology.—*Colidotea wallersteini* is named in honor of Dr. Barry Wallerstein, in acknowledgment of his work on the systematics and ecology of the Idoteidae and

in recognition of his long-standing friendship; furthermore, the resemblance in form is striking.

Discussion.—Of the 4 known species of *Colidotea*, 2 (*C. rostrata* and *C. edmondsoni*) share a unique derived character, the large cephalic tubercle. In addition to this synapomorphy, they have more general characters in common with one another than either shares with *C. findleyi* or *C. wallersteini*. No synapomorphies are recognizable to unite the latter 2 taxa as sister-species, so their cladistic relationship must be viewed as a trichotomy at this time. The character relationships of the known species of *Colidotea* are expressed in the cladogram in Fig. 6.

Because Hawaii arose as an oceanic island, *C. edmondsoni* most likely evolved there in isolation subsequent to a dispersal event from western North America. Its immediate ancestor was probably a free-living species that was also the parent taxon to the commensal *C. rostrata*. *Colidotea findleyi* and *C. wallersteini* can be derived from this same ancestral lineage. The latter is strictly a warm-temperate species, known only from northwestern Baja California and Guadalupe Island (Fig. 7). *Colidotea findleyi* is also a warm-temperate species, but exhibits considerable eurythermy in its ability to survive the warm summer months typical of the northern Gulf of California. The disjunct occurrence of *C. findleyi* on both the western coast of Baja California (and Guadalupe Island), as well as the restricted northern Gulf of California population, suggests that it may have entered the Gulf during a period of lowered oceanic paleoisotherms (i.e., Pleistocene glacial periods). Brusca and Wallerstein (1979b) and Wallerstein and Brusca (1982) have discussed the probability of such events, suggesting that the Pleistocene glacials and interglacials (and the associated latitudinal shifts in coastal isotherms) resulted in a series of vicariant events such that populations of temperate species were repeatedly trapped in the northern Gulf of California as latitudinal isotherms shifted from north to south and back. These events were probably responsible for the evolution of the various northern Gulf endemic species that have warm-temperate (Californian) sister-taxa. If this theory is correct, *C. findleyi* can most simply be envisioned as a sister-species of *C. wallersteini*, the 2 taxa being vicariant products of one of the earlier Pleistocene glacial episodes. Sympatry was later effected when a subsequent glacial event facilitated the escape of *C. findleyi* from the Gulf. The present interglacial period and relatively high coastal isotherms maintain the current disjunct distribution of *C. findleyi*.

Acknowledgments

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